Assessing the abundance and role of invertebrate communities in tropical soils: Aims and methods

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Macro-invertebrates have a major role in regulating soil processes in the humid tropics. Termites and earthworms are especially important in conserving the soil structure and mediating efficient nutrient cycling. Management practices often create situations in which these essential agents of soil quality have been destroyed or are represented by species which are not well adapted to the new soil conditions. It is thus important to assess macro-invertebrates communities in managed soils to make sure they are well adapted. If not, suitable practices including the facilitation of existing species, or the introduction of better adapted species may be envisaged. A simple method to assess the abundance and structure of soil macro-invertebrates is proposed and illustrated by two case studies.

Key words: Soil invertebrate communities land-use practices, sampling method.

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INTRODUCTION

In the tropics, more than 60 % of the area is covered by oxisols with low nutrient contents, low pH and limited organic reserves (Sanchez & Salinas, 1983). This mineral poverty sometimes goes along with poor structural properties when the clay content is low and/or the clays are of low quality.

Despite their apparent low fertility, these soils support very high levels of natural primary production. Biological systems of regulation ensure the maintenance of the physical structure, conservation of humic reserves and an efficient cycling of nutrients (Lavelle, 1984).

These systems consist of an energy source (mainly leaf litter, dead or living roots, and soil organic matter), micro-organisms (bacteria, fungi and actinomyceta) as the main decomposers, and macroorganisms (living roots and invertebrates) as regulators. The main function of such regulators is to create suitable conditions for microbial activity: they fragment the plant debris, mix the fragments with the soil and ingest them. These activities result in a modification of the physical properties of the debris (comminution) and the creation of suitable conditions for microbial activity (e.g. increase of the overall surfaces for bacterial attack and water availability). In some cases, the macroorganisms produce limited amounts of readily assimilable organic matter, such as root exudates or intestinal mucus of earthworms, which may enhance the microbial activity and, through a "priming effect", render these micro-organisms more able to digest the resistant complex organic compounds of the soil (see Jenkinson, 1966; Jenkinson *et al.*, 1985; Barois & Lavelle, 1986) (Fig. 1).

The importance of the role of soil invertebrates may vary with their abun-

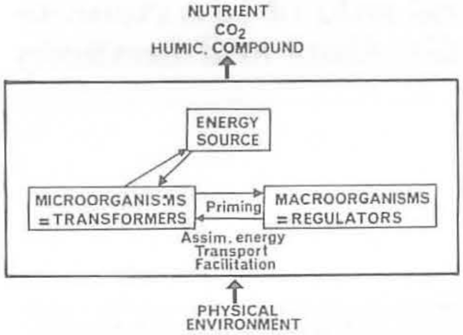

Fig. 1. - Biological systems of regulation in soils.

dance and taxonomic and functional diversity. Hence a study of soil fauna communities in natural environments may give a semi-quantitative evaluation of the role they play in soil processes. Comparative studies in adjacent disturbed and/or managed systems may point out changes in the abundance are structure of soil invertebrate communities. Subsequent disequilibria and/or decreased biological regulation result in damage to soil fertility. In such cases, it may be worth trying to improve the activity of soil invertebrates by modifying environmental conditions, or introducing species which are better adapted to the new environment.

A simple methodology to assess the abundance and expected role of soil macro-invertebrate communities is proposed here and illustrated by two case studies.

CHARACTERIZATION OF SOIL INVERTEBRATES

Soil invertebrates may be identified at many taxonomic levels (e.g. order, family, genus or species) or characterized by morphological or ecological properties which relate to the function they perform in the soil (e.g. the niche they occupy and the physical and chemical consequences of their activity).

Both classifications are complementary. Taxonomic identifications must be as accurate as possible; however identification keys are lacking so that in most cases, identifications by non-taxonomists will hardly reach the genus if not the family level. Furthermore, even if all the species could be identified, the function of each species has to be characterized using ecological classifications to allow inter-community comparisons.

A preliminary classification based on size (see e.g. Swift, Heal & Anderson, 1979) separates three groups of soil invertebrates with different modes of living:

- *microfauna* includes organisms less than 0.2 mm long (or 0.1 mm wide) which live in soil free water; they are Protozoa, nematodes and rotifers;
- *mesofauna* includes organisms less than 4 mm long (or 2 mm wide) which live in the litter or soil cracks and pores; they have an aerial respiration and move into the soil and litter without digging. They are mainly microarthropods and enchytraeid worms;
- *macrofauna* includes animals longer than 4 mm (or wider than 2 mm) which are easily located by the naked eye. They are most frequently active on the soil surface, but may move or live in the soil, in which case they have to dig temporary or semi-permanent burrows and tunnels for their movements.

At present, this last group is the only one that may be sampled and characterized by non-specialists since simple and easy-to-handle methods and ecological classifications are available for them only. It is also the most important as regards biomass and physical impact on the soil structure. Mesofauna have relatively lower densities while the role of the microfauna is much more dependent on soil conditions since they are not able to modify their environment by the building of specialised structures (see UNESCO, 1979; Swift *et al.*, 1979; Lavelle, 1983a).

The overall function of soil macroinvertebrates may be characterized by the feeding resource they utilise and their vertical distribution in the soil (Bouché, 1971; Lavelle, 1981):

- *epigeics* live and feed in the surface litter;
- *anecics* feed on surface litter but transport it to new localities; e.g. earthworms take litter into their subterranean galleries and termites transport it to their epigeic or endogeic nests;
- *endogeics* live beneath the soil surface and feed into the soil on soil organic matter. They may be subdivided into three categories according as they feed on soil which has a content greater than (polyhumics), equal to (mesohumics) or less than (oligohumics) the average of the upper 15 cm of soil.

IMPORTANCE OF SOIL FAUNA ACTIVITIES IN TROPICAL SOILS

Still to little is known about the role of invertebrates in humid tropical soils. Only fragmentary results have been obtained on important groups such as ants, Coleoptera and Myriapoda (see for example Levieux, 1983; Girard, 1983; Villalobos, 1985) and our knowledge of most micro- and mesofauna groups is restricted to a few estimates of their abundance (see Athias *et al.*, 1975; Lavelle 1983b). However, the role of termites and earthworms, which are currently the dominant groups, has been documented in a number of sites (see reviews in Lee and Wood, 1971; Lee, 1985; Josens, 1983; Lavelle, 1983b). A few selected examples may give an illustration of what their role may be.

Earthworms

In the humid grass savannas at Lamto (Ivory Coast), earthworm communities include 13 species of which 8 are abundant. Their feeding regime is mainly geophagous which is common in most tropical soils (Lavelle, 1983b). The mean density is 23.10^5 m^{-2} and biomass is 490 kg fresh mass ha^{-1}. They ingest annually 180 kg dry leaf litter and 1000 Mg dry soil ha^{-1} which contains 14.5 Mg organic matter. This is equivalent to one third of the overall soil organic matter (SOM) content of these soils, but 60 % of the SOM of the upper 10 centimeters (Lavelle, 1978). Nine percent of the ingested OM is assimilated, the remainder is passed out as faeces. However, the fate of the egested material will be very different from that of non consumed matter since the microbial activity in the casts may be inhibited, or most often increased, depending on the current intensity of mineralization. This regulation of earthworms over mineralization rates may last for several weeks and thus constitutes one major regulation system of microbial activity and nutrient release from SOM.

The effect of earthworms on the soil structure is important. The upper 15 centimeters of the soil profile are composed largely of earthworm casts which give the soil a resistant granular structure (Fig. 2). The production of 26 Mg. ha^{-1} of casts on the soil surface may constitute a resistant surface mulch and corresponds to the creation of 25 to 30 m^3 of spaces in the soil which may compensate for natural compaction.

In Nigeria, Aina (1984) estimated the volume of earthworm channels in the top 12 cm of a forest and an adjacent cultivated field. They represented 0.37 % of the soil volume in the former case and 0.02 % in the latter. The proportion of pores > 60 microns was greater by 30 % in the forest and 13 % under cultivation than in comparable plots where earthworms had been eliminated. As a consequence, the porosity of the soil in the presence of earthworms was more than 2.5 times greater in the forest and one third greater in the cultivated plot.

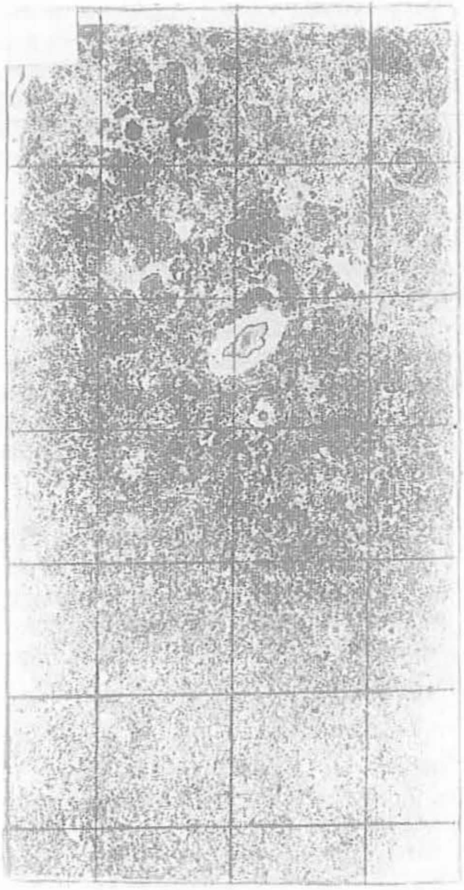

Fig. 2. - Thin section in a savanna soil (Lamto, Ivory Coast) showing the effect of earthworms on the soil structure (the squares are 5 x 5 cm).

Termites

In tropical forests as well as African dry savannas of the sudanian or sahelian zones, earthworms are less important and are absent where the annual rainfall is less than ca 800 mm and the dry season extends over more than 5 to 6 months. In these environments, termites generally become the dominant group of soil invertebrates. They often have a dramatic effect on the soil's physical structure and the cycling of organic matter and nutrients. The result of their activities may be very diverse since communities may include representatives of the different ecological categories: epigeic xylophages, anecic harvesters or growers of fungi and oligo- to polyhumic geophagous humivorous species. In contrast to earthworms they are not restricted to humid areas and their relative importance seems to increase from the humid savannas towards semi-humid (e.g. soudanian savannas in Africa) and semi-arid (e.g. sahelian) areas. Their importance also increases in forests where the water regime tends to be drier than in adjacent savannas and where leaf litter and woody material are on average more abundant.

Termites may ingest a significant proportion of the above ground plant production, between one quarter and one third of the litter produced in savannas according to Josens (1983) and up to 70 % in some sudanian savannas (Ohiagu & Wood, 1979). The litter they consume is taken into their nests where it is totally decomposed. The excreted mineral nutrients are incorporated with soil into their structures (nest walls, surface sheeting or subterranean chambers) only to be released as the structures erode. Hence the spatial and temporal pattern of nutrient release will be very different from unconsumed material (see Lee & Wood, 1971; Menaut *et al.* 1985).

The effect of termites upon the physical properties of soils may be very important through the construction of mounds, nests, galleries and surface sheetings. Nye (1955) calculated that a layer, 30 cm thick, could be deposited on the soil surface in 12,000 years through the breakdown of termite mounds, in central Nigeria, and Wielemaker (1984) has clearly demonstrated that some Kenyan soils have been formed by termites.

Termites generally select the finer size fractions, but with a great range of variations according to the soil texture and the species considered (Lee & Wood, 1971). The result is the development of a fine textured surface horizon without stones and gravels (Montgomery & Askew, 1983).

MINIMUM SAMPLING DESIGN

Assessing the abundance and functional structure of soil macro-invertebrate communities may be done with a simple and relatively non-time-consuming method. Dynamic extraction techniques, which rely on movements of animals as a response to physical or chemical stimuli, will be avoided because of their generally low efficiency in the conditions of tropical soils and their excessive selectivity.

Handsorting of relatively small unit samples (25 x 25 x 30 cm) has proved to be preferable, even when the density of small, brown coloured and/or immobile organisms is underestimated (Lavelle *et al.*, 1981; Lavelle and Kohlmann, 1984). The careful sorting out of small handfuls of soil over large plastic pans restricts this underestimation to an acceptable level and gives reproducible results which makes possible inter-site or inter-treatment comparisons (see the detailed procedure in Anderson & Ingram 1987).

The number of replicates should be sufficient to permit calculation of a representative mean, at least of the overall density. This can be checked by the simple graphic observation of the progressive stabilization of the mean as the number of replicates increases. In the Laguna Verde area (Mexico, Veracruz), a minimum number of 10 such samples has proved to be necessary to characterize one "homogeneous" site. According to conditions, three people are able to sort out two to five soil samples in six hours.

The replicates are located at 5 m regular intervals along a line whose starting point and direction may have been chosen randomly. However, such particular microhabitats as the foot of trees and the surroundings of emerging rocks or decaying logs should normally be avoided and may justify a separate study (Lasebikan, 1974; Lavelle & Kohlmann, 1984).

The invertebrates collected are counted by broad taxonomic units (Families or Orders) and weighed. However, when suitable expertise is available, more detailed identifications should be done. In addition to this taxonomic classification, the collected invertebrates may be divided into functional categories as defined by Bouché (1971) and Lavelle (1981).

This sampling design will give for each site three kinds of results:

- density and biomass of the different taxonomic units, and a quantitative estimate of the overall abundance and taxonomic structure of the macro-invertebrate community;
- functional structure of the community by comparing the relative contribution of the different ecological categories to density and biomass;
- spatial distribution: vertical distribution among above ground, litter, and successive 10 cm thick soil strata and horizontal patterns by calculating the aggregation index tested with a χ^2 test.

Comparison among different sites should be done using factor or principal component analyses (see e.g. Lavelle *et al.*, 1981).

TWO CASE STUDIES IN TROPICAL MEXICO AND PERUVIAN AMAZON FOREST

In the region of Laguna Verde (Veracruz, Mexico), 18 sites were sampled using the methodology outlined above (Anderson & Ingram, 1987). They represent a sequence of vegetation types ranging from the cultivated pastures to the original low tropical forest and oakwoods. The altitude varies from sea level to 800 m and two main soil types are found, sandy soils in the coastal plain and clay ones on the hill sides. The macro-invertebrate community was split among 30 taxonomic units. Five unit samples

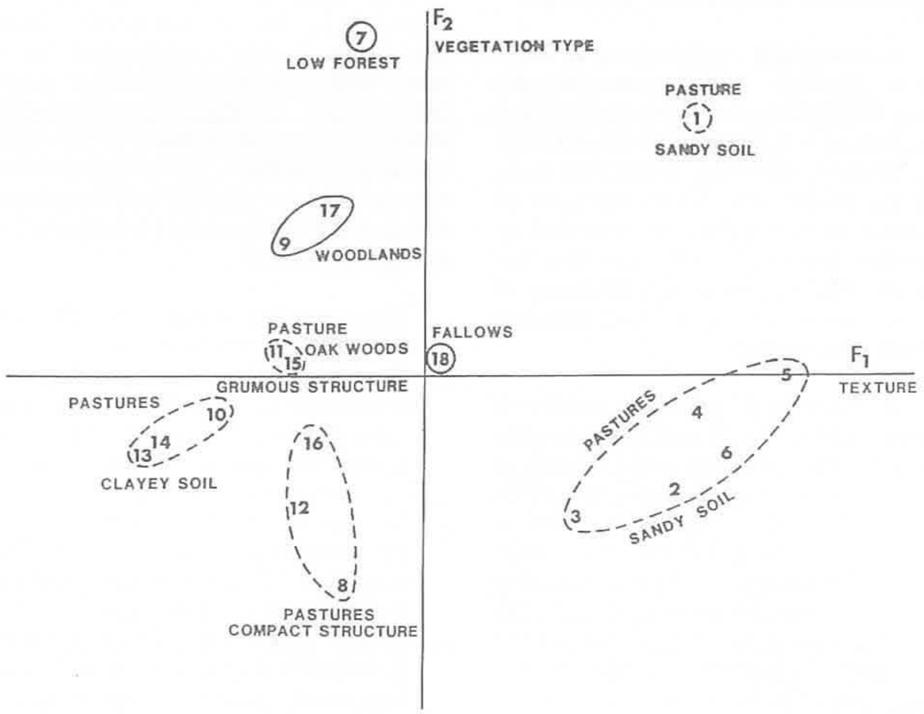

Fig. 3. - Factor analysis (principal components) comparing the communities of 18 different soil-vegetation systems at Laguna Verde (Veracruz, Mexico).

were taken in each site and grouped to constitute a single sample representative of the site. These 18 samples were then analyzed using a principal components analysis combined with a cluster analysis programme (Constel programme, Meyer, 1974). The main factors extracted were texture effects (21 % of the variance explained) and vegetation cover (11 %). Six main clusters were distinguished: three grassland types with respectively clay, loamy and heavy structure, fallows, low altitude tropical forests and woodlands with sandy soils (fig. 3). These groups differ essentially by their overall abundance and the relative proportion of earthworms, termites and Coleoptera.

Interestingly, these results are similar to the ones obtained in a previous study conducted in the same area with very time-consuming sampling techniques. The two main factors were the same but the total variance they explained (66 %) was twice as high as in the present study (Lavelle *et al.* 1981).

At Yurimaguas (Peru), soil macroinvertebrate communities have been compared in a primary forest and in three different types of soil management: traditional pasture, traditional low input rice and high input corn cultures (Pashanasi and Lavelle, unp.). In each situation, 10 unit samples were taken. The results show striking differences among the overall abundance, diversity and functional structure of the communities (Table 1). Deforestation results in a generally sharp decrease in diversity, but according to the type of land use, the remaining community may take different shapes. In pastures, the decrease in diversity is less than in the other two sites; the density decreases, but the biomass increases due to colonization by the opportunist peregrine earthworm species *Pontoscolex corethrurus*.

Table 1. - Abundance and diversity of the soil fauna in different types of land use at Yurimaguas (Peru) (Lavelle and Pashanasi, unp. data).

Type of use land	Number of samples	Overall density.m-2	Biomass g.m-2	N° taxon. units	% Biomass Termites	% Biomass Earthworms
Primary forest	10	4256	41.35	37	16.5	58.9
Traditional rice field (1 year)	10	3683	6.78	25	71,9	7.1
Traditional pasture	10	1768	96.88	26	1.1	96.
Improved pasture *(Brachiaria-Desmodium)*	10	915	127.93	25	0.01	96.2

In cultivated lands, the community is much more depleted, especially in the rice field where termites are dominant. The functional structures of the communities varies greatly as a consequence of these changes, with a rather equilibrated structure in the primary forest, dominance of endogeic polyhumics in the fields and mesohumics in the pasture (Fig. 4).

DISCUSSION

The two examples show that a fast, but reasonably accurate characterization of soil macro-invertebrate communities is possible with this simplified methodology. The main groups are identified and a semiquantitative estimate of their role is given by their functional structure. The effect of changes in the vegetation char-

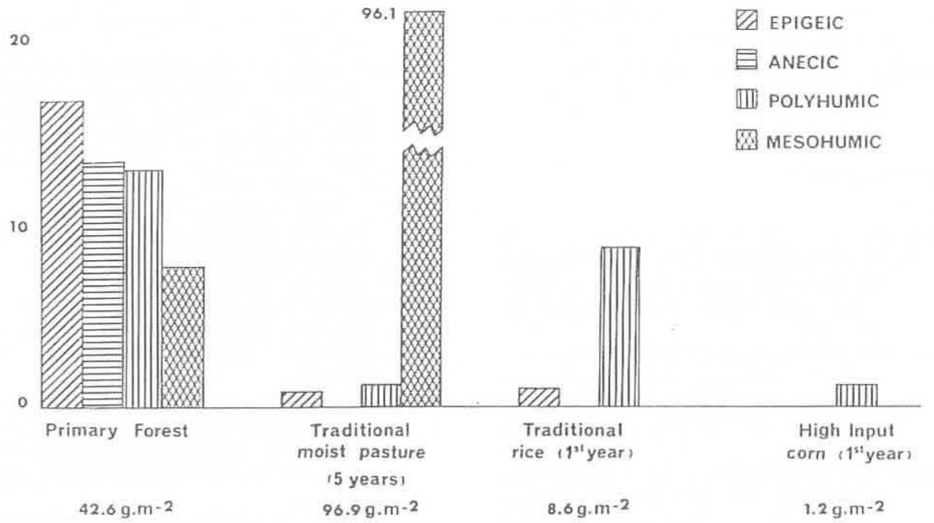

Fig. 4. - Functional structure of the soil fauna from the original primary forest and three different types of land use at Yurimaguas (Peru) (Lavelle and Pashanasi, unp. data).

acteristics and soil type (example 1) or different types of land use (ex. 2) may thus be evaluated. Further studies should concentrate on the description of the role of the main invertebrates and/or explain the modifications of the community structure.

In a further stage, manipulations may be envisaged if it is felt that soil fertility is decreased by the disturbances observed in the community. Minimum environmental conditions for maintaining important components of the fauna may be required and restored. As an example, such practices as mulching, interval cropping or using suitable covering plants may help to maintain an active litter-feeding fauna by providing buffered temperature and moisture conditions and energy sources. In some situations (e.g. the shift from a primary tropical forest to a pasture), the change in environmental conditions is such that an efficient community made of species previously living in the forest is unlikely to develop. Then, the introduction or the facilitation of adapted alien species may be a means of maintaining the soil structure and nutritive fertility; a possible example is the introduction of earthworm species from moist savannas or perturbed lands (e.g. *Pontoscolex corethrurus*) into pastures induced in formerly forested areas.

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